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ヌスビトハギ（広義）*Hylodesmum podocarpum* (DC.) H.Ohashi & R.R.Mill の種内分類群の中でシロバナケヤブハギ subsp. *fallax* f. *album* (Sugim.) H.Ohashi, ヌスビトハギ subsp. *oxyphyllum* var. *japonicum* (Miq.) H.Ohashi, シロバナヌスビトハギ f. *albiflorum* (Iwata) H.Ohashi, オキチハギ f. *decorum* (Iwata) H.Ohashi の新組合せを行なった．ヌスビトハギの変種ランクでの学名は *Desmodium podocarpum* var. *japonicum* (Miq.) Maxim. (1886) が最も早く発表されたのでこの変種形容語を使わねばならなかったが，Ohashi and Mill (2000) ではこれを見落としたので，訂正する．

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SINGH B. P.: Diversity of Vascular System in the Wall of Inferior Ovary in the Family Asteraceae

キク科下位子房壁における維管束システムの多様性（B. P. シン）

The Asteraceae, comprising about 1200 genera and 25000 species, is one of the largest family of flowering plants. The great homogeneity of the Asteraceae is displayed by their possession of capitulum inflorescence as well as the peculiar plan of floret which even when divorced from the mother plant could in no case be mistaken from anything else (Good 1956, Leppik 1960). To a student of evolutionary morphology of Angiosperms, Asteraceae flower presents several thoughts provoking problems. The evolution of collora, nature of pappus, placentation, floral evolution and inferior ovary are the subject of acrimonious debate and has already being reviewed in the earlier papers (Tiagi and Singh 1972, Singh 1973, 1994, 1998, 1999, Singh and Irvinder 1998a, 1998b) and would be referred to at appropriate places in the text. The present work was undertaken with a view to enlighten the evolution of vascular system in the wall of inferior ovary in the family Asteraceae.

Materials and Methods

In the present work, vascular anatomy of the flowers of 16 species of the family Asteraceae has been investigated. These are listed in Table 1.

Customary methods of microtechnique were used. Serial transverse and longitudinal sections of the florets and capitula were cut at the thickness ranging from 7 to 15 μm. Double staining with crystal violet and erythrosine gave satisfactory results. In all cases the floral buds were cleared by warming in 10 % solution of potassium hydroxide and subsequently in colorless lactic acid. The cleared buds were dissected under a stereomicroscope. This was found to be very useful in understanding 3-dimensional picture of the vascular skeleton. The author has investigated floral anatomy of approximately 250 species of the Asteracese, the plant specimens and slides are preserved in the Herbarium, Post-Graduate Department of Botany, S G N Khalsa College, Srigan-

Table 1. Taxa examined in the family Asteraceae in this study

No.	Taxon	Source
1	*Aster thomsonii* Clarke	Mussoorie
2	*Adenostemma lavenia* (L.) Kuntze var. *lavenia*	Jaipur
3	*Bidens biternata* (Lour.) Merr. & Sherff.	Ganganagar
4	*Carpesium abrotanoides* L.	Mussoorie
5	*Cirsium wallichii* DC.	Ganganagar
6	*Coreopsis drumondii* Tour. & Gray	Ganganagar
7	*Cosmos bipinnatus* Cav.	Ganganagar
8	*Cyathocline purpurea* (Con) Kuntze	Ganganagar
9	*Eclipta prostrata* (L.) L.	Ganganagar
10	*Glossocardia bosvallea* (L.f.) DC.	Dehra Dun
11	*Helianthus annus* L.	Ganganagar
12	*Lagascea mollis* Cav.	Jaipur
13	*Siegesbeckia orientallis* L.	Nepal
14	*Tithonia diversifolia* (Hemsl.) A.Gray	Gwalior
15	*Tricholepis radicans* DC.	Ganganagar
16	*Vicoa auriculata* Cass.	Mussoorie

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Terminology Used

The vascular skeleton of the Asteraceae flower needs an unambiguous terminology for preciseness of description. A single large vascular strand enters into the base of the floret from the stele of the capitular receptacle. It unusually consists of a few xylem elements surrounded by phloem. Rarely it is slightly modulated. This is termed as stelar strand (ss). The stelar strand gives out traces into the wall of inferior ovary. Whatever may be the number of traces inside the wall of inferior ovary it is by their splitting in its top that the vascular traces of all the floral leaves are organized. Thus, the traces inside the wall of inferior ovary are undoubtedly compound in nature. Though, the number of traces inside the wall of inferior ovary is highly variable, it is the interpretation of the morphological nature of the ten traces that is basic for the understanding of all the other traces. Five of these ten traces are usually strong and situated on radii, alternating with the radii on which the petals midribs stand above. Thus, the odd trace of this set is posterior in position. These are compound marginal trances (cmt) but for the convenience of description, these traces have been designated as 'alternipetalous'. The other five traces alternating with the alternipetalous traces and stand on the same radii as the midribs of the petals above are petal dorsal traces (pd). For the convenience of description these traces have been designated as 'antipetalous'. In some primitive forms ovary wall contains in all twenty trace flanked with secondary marginal traces (sm), alternating with the five strong alternipetalous traces.

The stelar strand after furnishing the traces into the wall of the inferior ovary becomes the central strands (cs). The central strand *in toto* becomes the ovular traces (ov).

Observations and Discussions

The chief evolutionary processes which have been operative in the modification of the vascular ground plan in the wall of inferior ovary of the Asteraceae are cohesion, adnation and reduction of the basal portion

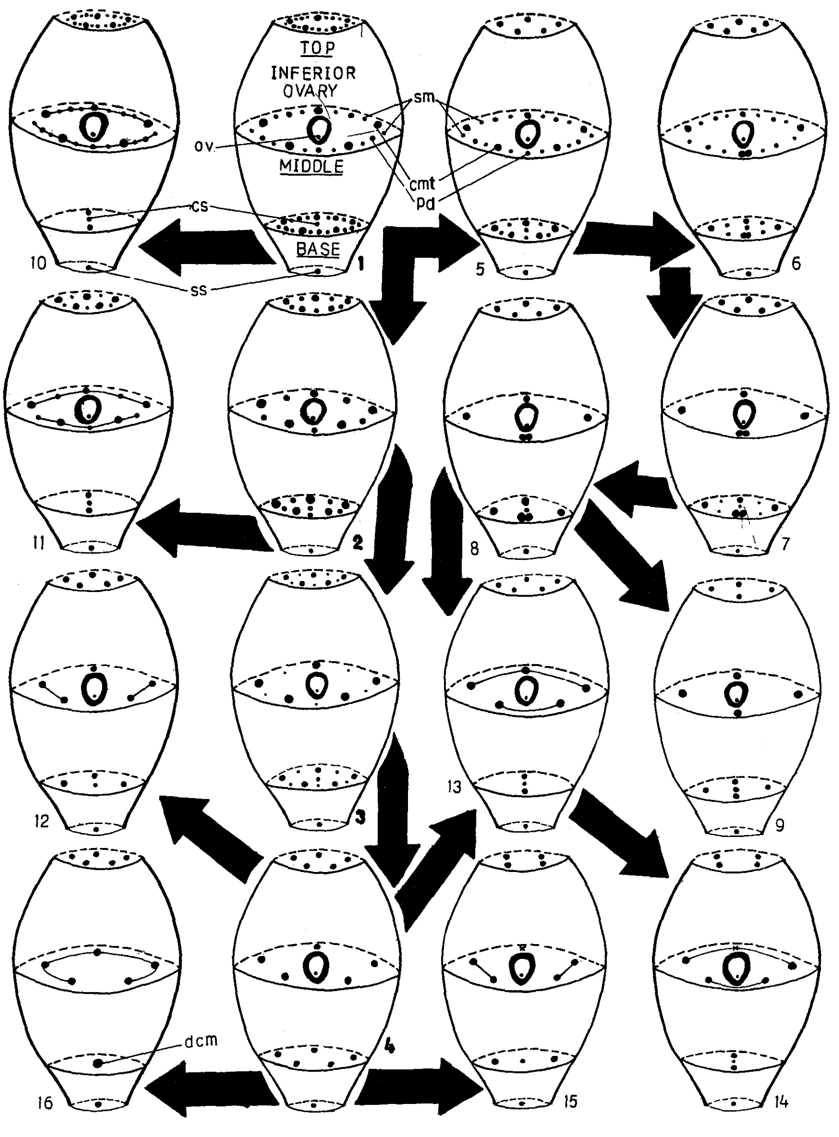

Fig. 1. Diagram showing the author's views on the evolution of the vascular system inside the wall of inferior ovary in the family Asteraceae (for explanation, see text). In Figures 10–16, in the middle portion of the inferior ovary the types of cohesion of vascular bundles inside the wall of inferior ovary are shown. Longisections of inferior ovaries of the Asteraceae are based on transverse sections of florets studies by the author (Singh 1973). The upper parts of the florets have been cut away. 1. Carpesium type. 2. Coreopsis type. 3. Trichokepis type. 4. Cosmos type. 5. Aster type. 6. Bidens type. 7. Siegesbeckia type. 8. Cirsium type. 9. Vicoa type. 10. Tichonia type. 11. Helianthus type. 12. Adenostemma type. 13. Lagascea type. 14. Eclipta type. 15. Glossocardia type. 16. Cyathocline type. Abbreviations: cmt, compound marginal traces; cs, central strand; dcm, decompound trace; ov, ovular trace; sm, secondary marginal trace; ss, stelar strand.

of the traces of the sepals, petals, stamens and carpels. The primitive flower in Angiosperms at large has a vascular cylinder, while a single vascular bundle supplies the base of ovary in most Asteraceae. However, in *Stenopadus* a cylinder of bundles is primitively present, which suggests evolutionary reduction to the single bundle has taken place early in the family (Carlquist 1961).

A comparative study of vascular pattern inside the wall of inferior ovary in the Asteraceae brings out a number of vascular patterns produced as a result of modification of certain basic types. The following types can be recognized and their interrelationship are analyzed.

Carpesium type, illustrated by *Capesium abrotanoides* (Fig. 1, 1). In this type a ring of twenty vascular traces is found inside the wall of inferior ovary and it consists of five strong alternipetalous compound traces (cmt) alternating with five triplets, each triplet consisting of medium-sized antipetalous petal dorsal (pd) flanked with small secondary marginal traces (sm). *Inula cappa* is more or less similar with suppression of some of the secondary marginal traces (Singh 1973). This type is considered as most primitive in the Asteraceae. All the other types appear to be derived from it.

Coreopsis type, illustrated by *Coreopsis drumondii*, can be derived from the Carpesium type (Figs. 1, 1–2) by suppression of ten weaker secondary marginal traces, so that a ring traces inside the wall of inferior ovary comprises only ten traces, five alternipetalous and five antipetalous in position. This type is also met in *Centrantherum anthermintincum*, *Elephantopus scaber*, *Trilisa odoratissima*, *Solidago virga-aurea*, *Flaveria rependa*, *Dicoma tomentosa*, *Sonchus arvensis* and *Sonchus oleraceous* (Singh 1973). In most of the cases belonging to this type, the antipetalous traces terminate blindly at the top of the inferior ovary and only the alternipetalous ones continue upwards.

Tricholepis type, illustrated by *Tricholepis radicans*, can be derived from the Coreposis type (Figs. 1, 2–3). In this type antipetalous traces are *ab initio* comparatively weaker or to become weaker during their upward course inside the wall of inferior ovary.

Cosmos type, illustrated by *Cosmos bipinnata*, can be derived from the Tricholepis type by complete suppression of the five antipetalous traces (Figs. 1, 3–4). Here there *ab initio* only five alternipetalous traces inside the wall of inferior ovary. This type is probably the most widespread in the Asteraceae.

All other types of vascular pattern inside the wall of inferior ovary can be derived from the four main types described above by the process of cohesion and reduction.

Aster type, illustrated by *Aster thomsonii*, can be derived from the Carpesium type by fusion of triplet in the basal region of the inferior ovary (Figs. 1, 1, 5). So the wall of the inferior ovary comprises only ten traces, five alternipetalous and five antipetalous in position. The antipetalous traces split into their original constituents, so in the middle of the inferior ovary twenty traces can be seen. The five triplet terminate blindly and do not reach the top of the inferior ovary and only the five alternipetalous traces continue upward.

Bidens type, illustrated by *Bidens biternata*, can be derived from the Aster type by the cohesion of two anterior alternipetalous traces to form a single strand which, however, in the upper part of the inferior ovary splits up into its original constituents (Figs. 1, 5–6). The four weaker traces, alternating with the four strong traces, split up into triplets in the middle region of the inferior ovary but all these disappear in its top. At the top of the inferior ovary are present only the five alternipetalous traces. This type is also seen *Amberboa ramosa* and *Saussurea canadensis* (Singh 1973).

A slight modification of this type is seen in *Siegesbeckia orientalis* (Fig. 1, 7) where the four weaker traces quickly disappear so they are not seen in the middle region of the inferior ovary. This condition is preliminarily designated here as Siegesbeckia type.

Cirsium type, illustrated by *Cirsium wallichii*, can be derived from the Siegesbeckia type by complete suppression of the antipetalous traces (Figs. 1, 7–8). The anterior strong traces splits up as in *Siegesbeckia orientalis*, so that in the top of the inferior ovary are present five alternipetalous traces.

Vicoa type, illustrated by *Vicoa auriculata*, can be derived from the Cirsium type by complete fusion of the two anterior antipetalous traces (Figs. 1, 8–9). So the ovary wall is with four alternipetalous traces and the flower in this case has become tetramerous.

Tithonia type, illustrated by Tithonia diversifolia, can be derived from the Carpesium type by visualizing cohesion of twenty traces into two medianly placed compound traces (Figs. 1, 1, 10). Such a view is substantiated by the fact that the two compound traces present in the wall of the inferior ovary split up into twenty traces in its top.

Helianthus type, illustrated by *Helianthus annus*, can be derived from the Coreposis type by the cohesion of the five posterior traces to form one and the remaining five on the anterior side to form another compound trace (Figs. 1, 2, 11). So the wall of the inferior ovary possesses two compound traces and an ovular trace in the lower part. These two compound traces break up into ten traces in the top of the inferior ovary. This type is also seen in *Verbesina oncophora* and *Ximensia encelioides* (Singh 1973).

Adenostemma type, illustrated by *Adenostemma lavenia* var. *lavenia*, can be derived from the Cosmos type by fusion in pair on each side between an anterior and lateral alternipetalous traces (Figs. 1, 4, 12), so that three traces are present in the lower part of the inferior ovary but five in its top. This type is also seen in *Eupatrium triplinerve* (Singh 1973).

Lagascea type, illustrated by *Lagascea mollis*, can be derived from the Cirsium type by cohesion of the posterior three traces into one compound trace, so that only two medianly placed compound traces are seen in the base of the inferior ovary. The desompound traces split up into its original constituents so that the five alternipetalous races are organized in the top of the inferior ovary (Figs. 1, 8, 13). This type can be also derived from the Cosmos type by cohesion of the posterior three traces into one and the anterior two into another compound trace (Figs. 1, 4, 13).

Eclipta type, illustrated by *Eclipta prostrata*, can be derived from the Lagascea type by suppression of the posterior alternipetalous trace (Figs. 1, 13–14). The two medinaly placed compound traces in the base of the inferior ovary fork to form four diagonally placed traces in its top. The flower in this case has become tetramerous.

Glossocardia type, illustrated by *Glossocardia bosvallea*, can be derived from the Cosmos type, firstly by loss of posterior alternipetalous trace and secondly by compounding on each side between an anterior and a lateral alternipetalous traces (Figs. 1, 4, 15). The laterally placed compound traces in the base of the inferior ovary fork to four diagonally placed traces in its top. Similar condition is also observed in *Chrysanthemum indicum* (Singh 1973) and the flowers in this type are tetramerous.

Cyathocline type, illustrated by *Cyathocline purpurea*, can be derived from the Cosmos type by cohesion of all the five alternipetalous traces into one decompound strand (Figs. 1, 4, 16). This decompound strand, however, breaks up into the usual five alternipetalous traces in the top of the inferior ovary. The disk floret in *Cyathocline purpurea* is staminate and the ovary is solid without ovule and loculus.

To conclude, therefore, the most primitive condition of the vasculature is seen in taxa like *Carpesium abrotanoides* where the wall of inferior ovary contains a ring of twenty vascular bundles. The bundles in the wall of inferior ovary appear to be gradually reduced to ten, eight, five, four, three, two or even one, in different taxa. In the staminate floret of *Cyathocline purpurea* the ovary position is solid with a single compound strand, looks like a thick pedicel which at its top bears the corolla with epipetalous stamens and the style making the flower look like a hypogynous one though genuinely epigynous.

The above mentioned types represent the major trends of evolution of the vasculature inside the wall of inferior ovary and are not intended to create an impression that a particular genus showing a particular type has originated from the one from which its vascular pattern has been derived.

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キク科16属16種について，下位子房壁における維管束走向を調べ，いくつかの基本型の修飾の結果としてできた維管束走向のパターンが認識され，それらの相互関係を解析した．下位子房壁における維管束走向の主要な進化のプロセスとは，萼片，花弁，雄蕊，心皮の維管束基部の同類合着（cohesion），異類合着（adnation），減数（reduction）である．その観点から，維管束走向の最も原始的な状態は子房内壁に20の維管束からなるリングが形成される，ヤブタバコ *Carpesium abrotanoides* のような分類群にみられるパターンにあると推定された．子房内壁における維管束の数は分類群により，10，8，5，4，3，2 あるいは 1 本というように次第に減数しているらしい．*Cyathocline purpurea* の雄性小花では子房は 1 本の複合維管束で満たされ，太い花梗のようにみえる．花梗のようにみえる子房の先端部には，花弁上雄蕊（epipetalous stamens）をもつ花冠と，真の下位子房でありながら花を上位子房のようにみせる花柱がある．

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